
FUNCTIONAL TRAITS COMPLICATE THE PICTURE OF TEMPORAL BIODIVERSITY CHANGE IN BIRD AND MAMMAL COMMUNITIES

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Abstract

Aim: Despite unprecedented environmental change due to anthropogenic pressure, recent work has found increasing dissimilarity due to turnover but no overall trend in species diversity through time at the local scale. Functional diversity provides a potentially powerful alternative approach for understanding community composition by linking shifts in species identity to the characteristics that confer ecosystem processes. Here we present the first multi-taxa, multi-system analysis of functional change through time.

Location: Global, with a North American focus

Time period: 1923-2014

Major taxa studied: Mammals, Birds

Methods: We paired thousands of bird and mammal assemblage time series from the BioTIME database with existing trait data representative of a species' functional role to reconstruct time series of functional diversity and composition metrics. Using generalized linear mixed models, we estimated general trends in those metrics and trends for individual studies.

Results: We found evidence of decreasing functional richness for mammal communities and increasing functional evenness in marine communities, but otherwise no overall trends in functional diversity metrics, which held even after correcting for changes in species richness. With the exception of those two trends, study characteristics such as taxa, realm, biome, or protection status did not distinguish between types of change exhibited by communities. At the study-level, there was substantial heterogeneity in the direction and type of functional change exhibited. We further did not find evidence to support multiple predictions for individual traits, including decreasing body size, dietary shifts, or changes in foraging strata.

Main Conclusions: General trends indicate that on the aggregate one type of functional shift is not more prevalent than the other across many taxa, biomes, and realms. Loss of functional richness in mammal communities indicates that they are on average faring worse than bird communities. At the study-level, the majority group of studies showed no species or functional trends, but other types of change were found for multiple studies, including studies experiencing changes in functional redundancy, increased species and functional richness, or loss of functional richness. With no one prevailing scenario of change, it will be critical to link change scenarios to ecological context.

Keywords biodiversity change · functional traits · global change · time series

1 Introduction

Ecological communities are experiencing unprecedented change as a result of anthropogenic pressures such as climate change, land use change, and invasive species. Impacts of these pressures are well documented at a global scale by an accelerating global extinction rate (1), and fundamental changes in some of the

most well-studied systems (e.g. coral bleaching, 2). At the local scale however, species diversity tells a different story. Recent syntheses of local trends in biodiversity over time have found no net change in local species diversity despite ongoing turnover (3–6) and evidence of significant shifts in community composition underlying consistent species richness (7–9). While communities are clearly changing, our most common species-based approaches do not fully capture the nature of that change.

Using general trends derived from limited data as a diagnostic for the state of biodiversity or directing conservation action is a topic of ongoing debate. Global analyses have been heavily criticized for geographic biases, lack of data in the most heavily impacted areas, and exclusion of individual studies’ ecological context (10–12). Many of these criticisms reflect limitations of ecological data on the whole, leading to a call for additional data not only to fill geographic and temporal gaps, but to flesh out key characteristics of communities (13, 14).

Functional diversity offers a potentially powerful addition to species-based approaches for detecting and describing community change by providing a mechanistic link between species’ response to environmental change (*response traits*) and the processes they perform (*effect traits*) (15–17). By describing the functional trait space, functional diversity metrics capture the disproportionate impact of losses or gains of functionally unique species. Functional diversity metrics may therefore illuminate joint responses from functionally similar species or communities undetectable by looking at species identity alone.

The expectation for functional diversity change across communities is not obvious from past work, and may or may not follow taxonomic trends (13). While loss of functional diversity is frequently cited as one of the most pressing concerns of the anthropocene (18–20), functional diversity may be maintained even when species are lost from a community (21, 22). Forecasts of functional loss range from negligible (23) to dire (24, 25). And while some observed trends show significant functional loss (26) others document no loss even in some of the most heavily impacted communities (27–29). On paleoecological time scales, the functional space shows mixed responses to environmental change and extinction events (30, 31), with significant impacts of species extinctions on functional diversity in some taxa and not others (32). For some time periods, functional diversity appears to be maintained for substantial portions of geological time (33). Contemporary, broad-scale examinations of functional change are limited to only a few taxa-focused studies, but show for example functional richness increases for both North American birds (34, 35) and ray-finned fishes, sharks, and rays (36).

We have stronger expectations for changes in the prevalence of some individual traits. For example, animal body size is expected to decrease as a result of climate change, a phenomena that has been documented in multiple taxa empirically and experimentally (37–41). There is some evidence that this holds true for birds (42), but the picture is likely more complicated for mammals, where urbanization may actually lead to larger body sizes due to novel food sources (43), even as megafaunal loss leads to on average smaller community body size. For dietary traits, recent work documenting insect declines (citation) points to potentially significant negative impacts on insectivorous animals (44–46). Predicted extinctions based on species-level vulnerability point to further dietary shifts, favoring increases in invertivorous species (47). Some systems also show significant shifts in the prevalence of different kinds of foragers in birds, for example loss of arboreal foragers in agricultural systems (48), and loss of neotropical understory foragers even in protect areas (49).

Here we leverage ongoing efforts to assemble functional trait data and recent computational advances to perform the first multi-taxa, multi-realm assessment of functional diversity and composition change through time. We focus on mammal and bird species as a subset of the world’s biodiversity of particular conservation concern that is heavily impacted by anthropogenic change. While examining trends in plants, invertebrates, and other vertebrate species is of equal interest, trait data for those taxa raise additional challenges such as limited and biased species coverage (50), a lack of accepted species-level means, and differences in the types of traits collected. To ensure comparability across taxa in trait type and data quality we therefore focus on mammals and birds. We include body mass, dietary, foraging and other behavioral traits that were intentionally selected to be representative of a species’ Eltonian niche, thereby summarizing the functional role they play in the community (51). An initial assessment of amphibian trends is included in the supplement, but excluded from general trend assessment here due to limited geographic coverage.

We assess thousands of mammal and bird functional diversity time series to determine whether or not the addition of functional trait data gives a clarifying picture of biodiversity change across communities. We present a few areas of change consensus across communities, and even more scenarios where functional trends are unexplained and warrant further theoretical and experimental examination. We assess functional diversity trends at three different levels: general trends across communities, trends for communities with similar characteristics (taxa, biome, realm, protection status), and trends for individual studies. We further evaluate

Table 1: Description of the traits included in the analysis broken down by categories at data type.

Trait	Category	Taxa	Data Type
Diet	Invertebrate	Bird and Mammal	percentage consumed
	Mammals and Birds		
	Reptiles		
	Fish		
	Unknown Vertebrates		
	Scavenging		
	Fruit		
	Nectar		
	Seeds		
	Other Plant		
Foraging Strata	Below water surface	Bird	percentage of use
	water surface		
	ground		
	understory		
	> 2m, below canopy		
	canopy		
	aerial		
Pelagic Specialist	yes	Bird and Mammal	binary
	no		
Nocturnal	yes		
	no		
Crepuscular	yes	Mammal	
	no		
Diurnal	yes		
	no		
Body Mass	-	Bird and Mammal	continous, in grams

evidence of key predictions for individual traits using trait-level compositional trends, including changes in mean body size, dietary traits, and foraging strata.

2 Material and Methods

2.1 Data

We obtained mammal and bird time series from the BioTIME database, a global repository of high-quality assemblage time series collected from the literature and ongoing monitoring efforts. Data is structured such that a study encompass all data collected following consistent sampling protocols and may contain multiple time series from separate locations. Time series represent full assemblages rather than populations of single species (31), and all time series include abundance of observed species. Following best practices for the database (52), studies with multiple sample locations were split into individual time series following a standardized spatial scale. Scale was set by a global grid with cell size determined based on the sample extent of studies with only a single location (see 31 for details on how sample extents were defined), with the area of each cell set to one standard deviation away from the mean of the single extent locations. The resulting cell size for our data was approximately 95 km². All samples from a study within a single cell were considered to be a single time series, and species abundances were combined for all samples.

We used trait data from the Elton Trait Database, which consists of species-level means for traits that represent species' multifaceted role in the community (51). Traits include: body mass, diet, nocturnality, forest foraging strata, pelagic use. With the exception of body mass, traits were broken down into percentage or binary use for each level of the trait type (Table 1).

In order to ensure taxonomic consistency across datasets, BioTIME species were paired with trait data based on their species identifier from the Integrated Taxonomic Information System database (retrieved 09-15-2020 from the on-line database, <https://doi.org/10.5066/F7KH0KBK>), obtained through the `taxadb` R package (53, 54). If more than one species in the assemblage data resolved to the same identifier, observations were

considered the same species. For trait data, traits for all species of the same identifier were averaged. Only studies for which at least 75% of species had trait data were included. In order to have a sufficient number of species to calculate functional diversity metrics, years with fewer than 5 species observed were also excluded. Sensitivity analyses were conducted for the trait coverage threshold and the duration of included time series.

Many studies had a variable number of samples within years. To account for this inconsistency in sampling effort we used sample-based rarefaction by bootstrap resampling within years for each time series based on the smallest number of samples in a year for that time series.

Our final dataset included 2,432 time series from 50 studies in 21 countries and 12 biomes and 6 different traits (Fig 1). Data came from both terrestrial and marine realms and five biomes (Global, Polar/Temperate, Temperate, Temperate/Tropical, Tropical). The earliest sample was in 1923 and the most recent was in 2014. While it is not possible with this data to directly assess the level of human impact occurring for each study, we include binary protection status as a coarse indicator of impact level. However, protected areas were almost exclusively from temperate terrestrial studies (with one tropical study), so results are confounded by multiple other study characteristics. For a full breakdown of studies and their characteristics, see the supplement. Our final dataset reflects many of the data biases that make global synthesis work challenging, including geographic bias, a bias away from areas currently under the greatest threat, and a bias towards shorter time series. We address these shortcomings and their potential impact on our results in the discussion.

2.2 Diversity Metrics

We calculated yearly metrics of functional and species diversity for each time series. Species-based metrics include species richness (S) and Jaccard similarity (J) as a measure of turnover. Jaccard similarity was calculated relative to the first observed year for a time series. A negative trend in J would therefore indicate decreasing similarity. We did not impose a correction for unobserved species as non-parametric estimators do not assign species identities to corrected richness values, and therefore could not be propagated to the functional diversity metrics.

Functional diversity metrics were calculated using the *dbFD* function from the *FD* R package (55). Here we report functional richness (*FRic*), functional evenness (*FEve*), and functional divergence (*FDiv*) which together describe three complementary characteristics of the functional space (56, 57). *FRic* assesses the volume of the trait space occupied by species in the community, with higher values indicating communities with species of more extreme trait values. *FEve* describes how species are distributed across the trait space and how abundance is distributed across species. Higher values of *FEve* indicate more even spacing of species in the trait space and individuals across species. *FDiv* measures the degree to which species and their abundances maximize differences in the functional space. Higher values of *FDiv* therefore correspond to communities where many highly abundant species are on the edges of the trait space.

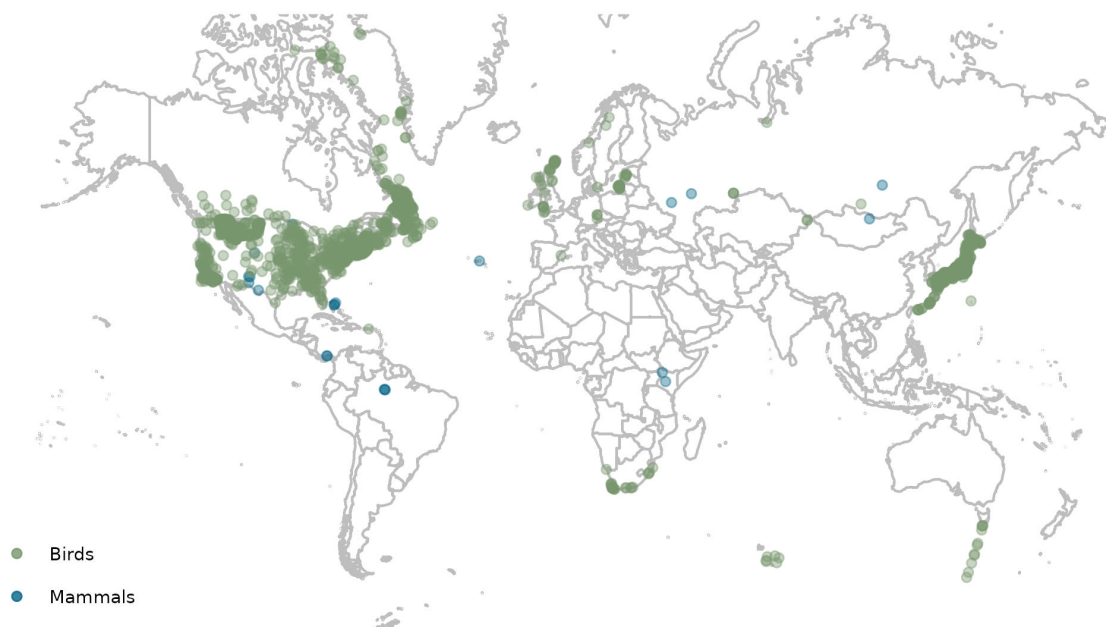
We also calculated the community-weighted mean (*CWM*) of all continuous traits to examine turnover in the distribution of each trait. Wholesale shifts in the trait space due to changes of trait means could occur even while the shape of the multidimensional trait space, as defined by functional richness, evenness, and divergence, is maintained. *CWM*'s are therefore a way to assess whether or not turnover is occurring and what the nature of the shift may be. Hereafter we refer to results for functional metrics in two groups: functional diversity metrics (*FRic*, *FEve*, *FDiv*) and composition metrics (trait *CWM*'s).

All available trait data for each study were included in functional diversity calculations with the exception of traits that were the same value for all observed species in the study. For variables with multiple levels each level was included as a separate trait axis. Continuous traits were z-score scaled to give each trait equal weight in the trait space (58, 59). Before calculating diversity metrics, *dbFD* reduces the dimensionality of the trait space by performing *PCoA*. We limited the number of included *PCoA* axes to the maximum number of traits that fulfills the criteria $s \geq 2^t$, where s is the number of species and t is the number of traits. This restriction allows for enough axes to capture the trait space while maintaining computational feasibility (60). Metrics incorporated weighting based on species abundance.

2.3 Null Models

To assess functional change independent of species richness we calculated the standardized effect size (*SES*) for each of the three functional diversity metrics (*FRic*, *FEve*, *FDiv*) from null estimates (61). Null model corrections allow us to assess the degree to which the observed functional diversity metric deviates from the value expected by chance in a randomly assembled community. Null estimates were calculated for each rarefied sample by randomly sampling species from the species pool for each year and randomly assigning

A



B

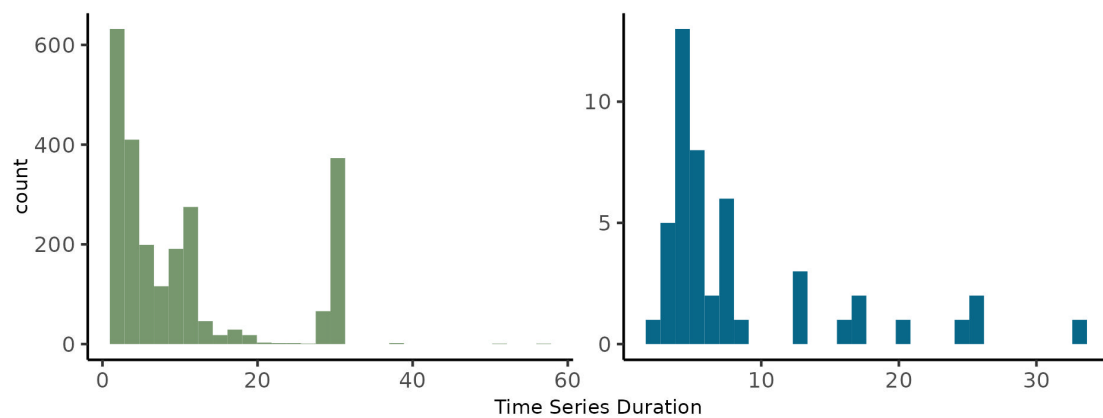


Figure 1: A) Map of time series locations with points colored by taxa, and B) histograms of time series duration broken down by taxa.

observed abundances to species. Species pools were unique for each time series and included all species observed over the course of sampling, therefore accounting for geographic restrictions in species availability. This process was repeated 500 times to get an estimate and standard deviation of the null expectation for the metric for each rarefaction sample for that time series. We used these values to calculate SES using the following formula: $SES = [F_{obs} - mean(F_{null})] / SD(F_{null})$. We then calculated the median SES estimate for each metric from all the rarefaction samples for a time series. SES estimates can be interpreted as how much of the functional characteristic (richness, evenness, divergence) was observed beyond what was expected by chance for a community of that species richness. This approach will be less accurate for shorter time series, as we likely will not have captured all available species in the true species pool, but it is impossible to know whether the mean estimate from the null model is an over or under estimate without knowing the functional characteristics of the missing species.

2.4 Analysis

We estimated general trends across bird and mammals communities for each diversity metric using a linear mixed effects model with a random slope and intercept for each study and each time series nested within the study, methods which deal well with the inherent imbalances in our data. We fit 18 individual CWM models, one for each trait included in the analysis. All time series with data for a given trait were included in the corresponding CWM model. We estimated study level trends using individual linear models. For studies with more than one times series we fit a random slope and intercept for time series. Some study-level models could not be fit for five studies for at least one metric due to data limitations, but those studies were still included in the general models. They represented 13 of 1350 study-level models fit for each metric. For further details see the supplement. Where appropriate, response variables were \log or $\log(x + 1)$ transformed to better fit model assumptions of residual normality.

To test for trends within and between different levels of taxa, biome, realm, and protection status we fit separate models with each of those factors added as a predictor interacting with time to the original model structure. We estimated within-level slopes and calculated between-level contrasts using the *emmeans* package (v1.8.2, 62). For some levels of the categorical variables we did not have a sufficient number of studies to estimate a general trend, we therefore refrained from interpreting results for levels where there were fewer than three studies. We assessed the impact of time series duration and start year on study-level trends using linear models with duration and start year as predictors. All models in our analysis were fit using the *lme4* (v1.1-30) package in R (v4.2.3) and p-values were calculated by Satterthwaite's degrees of freedom method using the *lmerTest* (v3.1-3) package with a significance level of $\alpha = 0.05$ (63–65).

3 Results

We found no significant overall temporal trend in species richness or functional diversity metrics including functional richness, evenness, or divergence (observed or corrected) (Fig 2). We did find a significant overall decrease in Jaccard similarity, indicating accumulating changes in species composition. Non-significant overall temporal trends indicate that although some studies experience increasing or decreasing trends, the average trend across studies was not significantly different from zero (Table 2). Within-group trends for different taxa, biomes, realms, or protection statuses were also non-significant for richness and functional diversity metrics, with the exception of a significantly increasing trend for functional evenness of marine studies, and a significantly decreasing functional richness slope for mammal studies. However, trends were not exhibited for the corrected metric indicating that differences in functional diversity metrics were largely due to changes in species richness. The general trends for CWM models were similarly not significant, with a significant positive trend for only percentage of fish in diet composition.

We did find significant differences between taxa, realms, and biomes for Jaccard similarity and some of the CWM's. For example, while Jaccard similarity was decreasing in the general trend and there were significant within group slopes for Mammals, Birds, Terrestrial, Temperate, and Tropical communities, there was no significant slope for the marine realm, indicating that the general trend is mostly driven by turnover in terrestrial communities. We also found a significant decrease in Jaccard similarity in unprotected areas only, with no trend for protected areas. We found significant dietary shifts across communities, with a significant general trend of increasing fish consumption, which was also reflected in increasing fish consumption trends for Bird studies and Temperate studies. We found a significantly increasing trend in nectar consumption for Temperate studies but a significantly decreasing trend for Tropical studies. We found significantly decreasing trend for vertebrate consumption in Marine studies and Tropical studies.

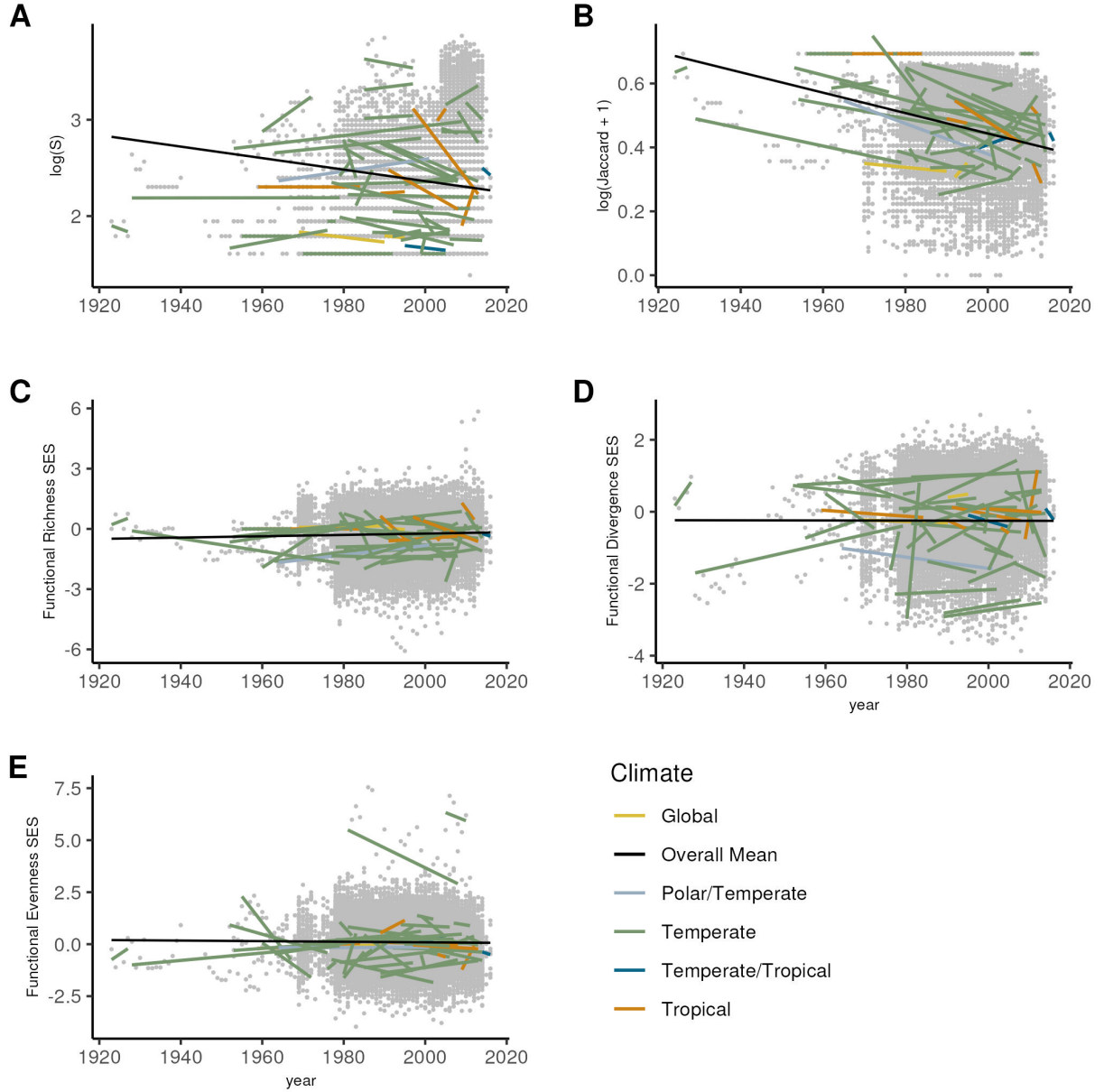


Figure 2: Plots of time series-level trends with line color corresponding to climatic region, with data points in grey and the overall mean slope for a metric in black for A) log species richness, B) Jaccard similarity, C) Functional Richness SES, D) Functional Divergence SES, and E) Functional Evenness SES

Table 2: Model estimates and statistics for general trend models for species richness, Jaccard similarity, and corrected functional diversity metrics. Additional model estimates, including CWM models, can be found in the supplement.

metric	effect	grouping	term	estimate	std.error	p.value
SES_FDiv	fixed		Intercept	-0.25	0.11	0.03
			Year	0.00	0.04	0.96
	random	study	SD Intercept	0.60		
			SD Year	0.11		
			Corr(Intercept, Year)	-0.16		
		time series within study	SD Intercept	0.60		
			SD Year	0.23		
			Corr(Intercept, Year)	-0.01		
SES_FEve	fixed		Intercept	0.10	0.17	0.56
			Year	-0.01	0.02	0.62
	random	study	SD Intercept	1.08		
			SD Year	0.04		
			Corr(Intercept, Year)	-0.53		
		time series within study	SD Intercept	0.40		
			SD Year	0.17		
			Corr(Intercept, Year)	-0.21		
SES_FRic	fixed		Intercept	-0.26	0.07	<0.001
			Year	0.04	0.04	0.35
	random	study	SD Intercept	0.29		
			SD Year	0.11		
			Corr(Intercept, Year)	-0.27		
		time series within study	SD Intercept	0.54		
			SD Year	0.18		
			Corr(Intercept, Year)	0.06		
log(Jaccard + 1)	fixed		Intercept	0.46	0.02	<0.001
			Year	-0.03	0.00	<0.001
	random	study	SD Intercept	0.09		
			SD Year	0.02		
			Corr(Intercept, Year)	-0.36		
		time series within study	SD Intercept	0.08		
			SD Year	0.02		
			Corr(Intercept, Year)	0.05		
log(Species Richness)	fixed		Intercept	2.40	0.10	<0.001
			Year	-0.06	0.05	0.17
	random	study	SD Intercept	0.64		
			SD Year	0.27		
			Corr(Intercept, Year)	-0.70		
		time series within study	SD Intercept	0.21		
			SD Year	0.09		
			Corr(Intercept, Year)	0.34		

At the study level, 16 of 50 studies exhibited a significant trend in species richness and 11 exhibited significant turnover. For uncorrected functional diversity metrics, 25 of 50 studies exhibited a trend in a least one metric, and 15 of 50 studies exhibited a significant trend for at least one **corrected** metric (Table 3). In general, there were more significant trends for uncorrected metrics, with some disappearing after correction, indicating that those trends were likely due to changes in the number of species. Hypothesis testing for study-level trends is likely affected by multiple testing issues and some trends identified as significant are therefore potentially spurious. Rather than interpreting changes in specific studies, we present these results as a general picture of the kinds of trends experienced by communities.

Study-level slopes were significantly related to start year of the time series for Jaccard similarity and functional evenness models, both of which had significantly more negative slopes with more recent start year. No functional diversity metrics were significantly related to the duration of the time series.

Table 3: Number of studies that experienced a significant trend in each calculated metric out of 50 total studies.

	S	Jaccard Similarity	FRic	FEve	FDiv	SES FRic	SES FEve	SES FDiv
+	7	0	7	5	3	4	4	3
-	9	11	8	6	5	2	6	2

We assessed the sensitivity of general trend results to major data processing decision by rerunning models with increasingly conservative subsets of the data. Trends for Jaccard similarity and fish consumption were not sensitive to either time series duration or trait coverage. After excluding time series with less than three years we found an increasing trend for body mass that remained after excluding time series of less than four and five years. We also found a decreasing trend in functional richness for models with a minimum of three years and a minimum of five years. A decreasing functional richness trend was found for models with a min of 85% trait coverage, but not the other two coverage levels. A complete list of models run in the sensitivity analysis and their results can be found in the supplement.

4 Discussion

Our study represents the largest broad-scale multi-taxa assessment of functional change through time to date, giving a first look at aggregate and local trends in functional diversity in mammal and bird communities. Our results show that the addition of functional traits illuminates a few consistent functional trends across communities, but largely complicates rather than clarifies the story of biodiversity change. While the characteristics of species clearly matter, instead of unifying the nature of communities' change, they more often distinguish them. In general, we found a few areas of consensus for models where communities were aggregated (general trends, trends by taxa, biome, realm, protection status), and vast heterogeneity for study-level models.

4.1 Evidence of consensus

The most stark area of consensus was the lack of general trend aggregating across communities. We did not detect an overall trend in any functional diversity metric, corrected or uncorrected. As with previous species-based syntheses, we also found no overall trend in species richness accompanied by increasing dissimilarity through time (31), indicating that non-significant trends in functional metrics are consistent with similar well-documented species derived trends. We found significant turnover for all biomes, realm, and taxa except for marine studies, which stands in contrast to other global estimates of biodiversity change that found higher turnover in marine systems than terrestrial (52). However, previous global estimates are dominated by fish communities which we exclude here and may be driving the overall trend while disguising relative stasis in marine bird and mammal communities.

We found evidence of functional richness loss in mammal studies, with a loss trend significantly different from zero and significantly different from the trend for birds, indicating a potential loss of functional capacity in these communities. This result is consistent with previous work linking anthropogenic drivers such as habitat loss, poaching, and human modification and development to loss of functional diversity in mammal communities across the globe (66–68). However we did not find trends outside the random expectation for species loss, in contrast to expectations for multiple continents based on IUCN risk categories (66). In general, functional capacity of mammals showed greater declines than bird communities.

4.2 Areas of incongruence

The addition of functional trait data illuminated multiple areas where a synthesis approach is incongruous with system-specific studies or simply unexpected. For example, results for protected areas were surprising given the assumption that protection insulates communities from functional degradation. The only difference we found between protected and unprotected areas was significant turnover occurring outside protected areas and no significant turnover inside protected areas. Rather than the result of protection itself, this is likely due to the fact that the majority of studies were from terrestrial, temperate studies where turnover is known to be lower (52). While things may generally be more static within protect areas, the functional dimensions of protected communities fared no better or worse on average than their non-protected counter parts. Looking

at individual studies, there is a mix of both losses and gains in almost all functional diversity and composition metrics across communities found in protected areas.

We also found evidence of increasing evenness for marine studies, which was not predicted by previous work in marine systems. The empirical link between changes in evenness and ecosystem process is the most poorly studied of the metrics, however theory indicates that increased evenness improves function and stability (69), as the dominance of one or a few species makes function sensitive to the ability of those species to respond to environmental change (57, 70). Further, there is some evidence that maintaining evenness is important for supporting multifunctionality in communities (71). An increase in evenness is therefore a positive indicator for these communities, despite the fact that marine bird and mammal communities are some of the most threatened communities in the world. Still, this result may be a function of data limitations as the majority of marine studies are of seabird communities (7 of 9), so the general trend may be an early indicator of pay off from investments in sea bird recovery also found in recent species-based work (72).

Our results were also inconsistent with all predictions for changes in trait prevalence, including foraging strata, body size, and dietary traits. We found no changes in the prevalence of different foraging strategies, despite documented losses of understory birds in the neotropics and some evidence that agricultural incursion particularly threatens arboreal species. Those shifts may therefore be the result of specific contexts and not generalizable to bird communities across the globe. We found no evidence of general trends in the CWM for body mass for birds or mammals, indicating that either body size is not changing significantly due to climate change, opposing pressures such as urbanization are overshadowing climate change impacts, or more likely current shifts are happening at an intraspecific level and have not yet propagated to the species losses that would be captured by our data. Further, many of the studies in our dataset draw from areas that may have experienced significant loss of large-bodied species before the observation window, with contemporary loss rates slowing (73). Trends could be significantly different for the same time periods in regions of sub-Saharan Africa, for example, which has poor representation in our dataset but where megafauna exist on the landscape and are increasingly threatened (74).

Rather than declines in insectivory and increases in invertivory predicted by previous work, we instead found changes in the degree of consumption of fish, nectar, and vertebrates. Increases in fish consumption for bird and temperate studies may be the product of increased availability of easy fish from commercial fishing operations or the stocking of inland waterways for sport fishing. However, fisheries also have negative impacts on waterbirds through competition for fish or bird mortality due to by catch, making these results surprising. Decreases in nectar consumption for tropical studies is likely due to declines in bat species, as 4 of the 5 tropical studies are for mammals and bats were the only nectar consuming mammals sampled in our data. Interpretation of the increases for temperate studies is less clear, as temperate studies included many bird communities with a variety of nectar consumers. Similarly, decreasing trends for vertebrate consumption in marine and tropical studies are not obviously consistent with known changes in those contexts and warrant further examination.

4.3 Study heterogeneity

At the study-level, our results run contrary to our hope for a clearer picture of biodiversity change through a functional lens. The lack of general trend in functional diversity metrics belies a huge range of positive and negative trends at the study-level in both species and functional metrics. For example, it appears at the aggregate level that species turnover does not translate to functional turnover based on a lack of trends in CWM's. However at the study-level, all studies experiencing species turnover are also experiencing significant turnover for multiple individual traits, there is simply no consistency across communities in the kind of turnover occurring to be manifest in general trends.

In order to simplify discussion, we will talk about the implications for ecosystem process and vulnerability for communities grouped by their concurrent change in corrected functional diversity metrics, species richness and turnover split into positive, negative or no trend. While there are over 150 possible combinations of change direction (or no change) in the 5 metrics, we discuss here the six scenarios that occurred in more than one study: no change, species loss or gain only, loss of functional evenness, species richness loss with species turnover, and increase in species and functional richness accompanied by significant turnover. We focus on these scenarios to combat potential spurious results due to multiple testing, as it is unlikely all observations of the same scenario are due to false positives.

The majority group of studies (17 studies) exhibited no trend in any species or functional diversity metric. Contrary to the expectation due to anthropogenic and global change stressors, these communities do not show significant changes over the course of the observation window. Studies in this group span the distribution

of study durations excluding only the very longest running studies, with the longest no change time series lasting 23 years. They also included both bird and mammal studies and only four were located in protected areas, indicating that the lack of trend is not restricted to a specific ecological context or those communities most insulated from human impact.

The lack of trend could be the result of multiple possible scenarios. First, these may be communities resisting perturbations or simply not experiencing significant perturbations. Given the studies in this group come from all possible taxa, realms, biomes, and protection statuses, evidence points to communities resisting perturbation, offering some hope that there are areas of the globe where communities are fairing well for now. Alternatively, these may be communities that have experienced or continue to experience significant stress, but lost species or functional diversity outside the observation window. This could be true particularly for North American mammal communities where trophic downgrading and megafaunal losses occurred hundreds of years ago (75). Third, these communities may be experiencing directional shifts undetectable by available data. For example, species-level trait data does not capture intraspecific shifts in the trait space, which can represent significant changes in the functional space as a whole and impact maintenance of ecological processes.

Three of the groups fit under the broad umbrella of changes in redundancy. By definition, if a community gains or loses species while functional diversity metrics are unchanged, those species represent an increase or decrease in redundancy, so we include communities exhibiting gains (2 studies) or losses (5 studies) in species richness with no change in functional metrics or turnover and species richness loss with significant turnover (2 studies) in this umbrella. For communities exhibiting loss of redundancy (declining species richness), ecological processes are likely being maintained, but capacity to respond to future stressors is reduced (76). These communities are actually fairing better than expected looking at species-based metrics alone, but are also in a precarious position for maintaining ecological function into the future (77). Conversely, communities exhibiting an increase in redundancy (via an increase in species richness) are becoming better positioned to respond to future stressors, but are not actually expanding their functional capacity as may be assumed by looking at species gains alone (78).

The next group of studies (3 studies) exhibit an increase in species richness and functional richness with significant turnover. While these communities are losing some species that are functionally redundant or functional analogs of species additions, they are gaining even more species that expand the functional space. These communities have a hopeful trajectory, as they are improving their functional capacity and potentially their functional redundancy, likely leading to robust future ecological function. Notably, the studies that exhibited species richness increases were exclusively from terrestrial, temperate (sometimes temperate/polar) bird communities and occurred in countries where there has been a significant investment in conservation over the last few decades (United States, Canada, Sweden). Our results are consistent with other functional work in these regions, showing increases in species richness and functional diversity for North American breeding birds over the last few decades after a period of decline (35), and loss of common, functionally general species even as rare species are increasing in North America and Europe (79–81).

The final group (3 studies) exhibits decreasing functional evenness. These communities are of particular concern not just because of the role evenness plays in maintaining functionality, but because of increasing evidence evenness is more sensitive to environmental change than species richness (69). Formal tests of evenness changes as an early warning signal of more catastrophic shifts in functional diversity will be critical next step for understanding the full implication of evenness loss for ecosystem processes.

While the majority of studies fell into one of the groups discussed in detail above, 25% of the studies exhibited some different combination of change in metrics, underlining the vast heterogeneity of realized change scenarios. We have an indication of the ecological characteristics most likely to lead to some of the change types (e.g. temperate bird communities are gaining species and functional richness), but most types of change are exhibited across many different kinds of communities. Identifying key factors mediating the kind of biodiversity change a community experiences is critical for identifying areas of conservation concern and extrapolating results to areas where functional trait data may not be available. While it is tempting to draw a one to one line between the degree of human impact and loss of functional integrity (in the form of functional redundancy and richness), that relationship is not borne out by our rough metric of human impact (protection status) or previous taxa-specific or single community work, which is largely mixed (26, 82–84).

Study-level results also illustrate the relationship between species turnover and functional turnover. For all studies exhibiting increasing dissimilarity through time (11 studies), there were multiple significant trend in functional composition (CWM's) and diversity metrics. However, there was little consensus in the types of shift, as indicated by lack of general trends for most metrics.

4.4 Policy Implications

While we found no over all trends in functional metrics, our results should not be interpreted as an indication that the ongoing biodiversity crisis is less severe than previously described, or that there is no concern for functional change as a result of anthropogenic impact. In fact, study-level trends indicate quite the opposite, that functional shifts with negative or yet unknown implications for ecosystem processes may be going undetected by common species-based approaches. For example, loss of evenness in communities with constant species richness may be an first sign of a community being impacted by environmental change, with negative implications for stability and function.

One of the biggest threats to biodiversity is the wholesale conversion of natural areas to urban or human-dominated landscapes (85). Typical long term monitoring such as those included in our study stops before this conversion occurs, leaving the resultant precipitous declines in biodiversity unrecorded (10). This is a known issue with the culture of long term monitoring, and our results should not be removed from that context. Rather, this studies captures communities that are likely experiencing a degree of human intervention, but are still largely nature-dominated.

4.5 Future Work

The addition of functional trait data to the biodiversity change conversation is yet another illustration of how critical context is for understanding ecological patterns [catford2022; spake2023]. Here we assessed how key community characteristics such as biome, realm, taxa, and protection status may partition variation in the functional trends exhibited and found that, on the whole, these broad classifications did not seem to make the picture of change clearer. Further work linking specific ecological contexts to types of functional change will be critical for identifying new areas of concern, especially when those communities may not otherwise be showing significant changes in species richness. The identification of contexts where functional change is most likely occurring will be a significant asset in directing the future collection of trait data, the main barrier for taking a functional approach to biodiversity change.

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